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The Behavioral Immune System: Implications for Social Cognition, Social Interaction, and Social Influence

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Abstract

The "behavioral immune system" is a motivational system that evolved as a means of inhibiting contact with disease-causing parasites and that, in contemporary human societies, influences social cognition and social behavior. In this article, we provide an overview of the behavioral immune system and how it works, along with a review of empirical research documenting its consequences for a wide range of social psychological phenomena—including person perception, interpersonal attraction, intergroup prejudice, social influence, and moral judgment. We also describe further consequences for health, for politics and public policy, and for cultural differences. Finally, we discuss a variety of broader implications—both practical and conceptual—and identify some important directions for future research.

Keywords: behavioral immune system, person perception, prejudice, social categorization, attraction, sexual behavior, social influence, moral judgment, attitudes, health, culture.

1. Introduction

Contemporary human behavior is influenced by motivational systems that evolved over many millions of years. For instance, there are evolutionarily ancient motivational systems associated with needs for self-protection, affiliation, acquisition of mates, and provision of care to offspring (Kenrick, Griskevicius, Neuberg, & Schaller, 2010; Kenrick, Neuberg, Grisckevicius, Becker, & Schaller, 2010). These motivational systems are activated by perceptual and inferential cues; and, when activated, they have implications for many different kinds of social psychological phenomena. For example, the self-protective motive has implications for face recognition, social categorization, stereotype activation, and conformity to majority opinion (e.g., Becker, Anderson, Neuberg, Maner, Shapiro, Ackerman, Schaller, & Kenrick, 2010; Griskevicius, Goldstein, Mortensen, Cialdini, & Kenrick, 2006; Schaller, Park, & Mueller, 2003; Miller, Maner, & Becker, 2010). And when mating motives are activated, there are consequences not only for mating behavior, but also for prosocial behavior, interpersonal aggression, risky decision-making, and strategic non-conformity (e.g., Ainsworth & Maner, 2012; Baker & Maner, 2009; Griskevicius et al., 2006; Griskevicius, Tybur, Sundie, Cialdini, Miller, & Kenrick, 2007). The take-home message is not merely that these motives influence social cognition and behavior, but that they do so in a wide variety of ways—many of which are subtle and nonobvious.

Within this scholarly tradition, there has recently emerged a burgeoning body of research on a motivational system that appears to have evolved as a means of facilitating behavioral prophylaxis against infectious diseases—a sort of "behavioral immune system" (Schaller, 2015; Schaller & Park, 2011). When activated, this motivational system has implications for a broad range of social psychological phenomena, including person perception, interpersonal attraction, intergroup prejudice, social influence, and moral judgment. These psychological outcomes have further consequences—for health, for politics and public policy, for cultural differences, and for additional long-term societal outcomes too.

In this article, we provide an introduction to the behavioral immune system and how it works, along with an overview of empirical evidence documenting its wide-ranging influences on social psychological phenomena. We also discuss some further implications, both practical and conceptual. And, finally, we identify a set of important questions about this motivational system—and its implications—that remain unanswered and that will, we hope, inspire future research.

2. Conceptual Background on the Behavioral Immune System

We begin with a bit of background. In this section, we first draw upon relevant research in the biological sciences in order to establish the conceptual plausibility of a distinct motivational system that evolved as a means of facilitating the behavioral avoidance of potential infection. We then turn our attention to psychological research that empirically implicates the existence of such a motivational system in humans, and sets the stage for our review of the many ways in which this system influences social cognition and social behavior.

2.1. Theory and Research within the Biological Sciences

A conceptual argument for the existence of the behavioral immune system begins with the observation that disease-causing parasites—bacteria, viruses, helminths—have been prevalent within human and pre-human populations for many millions of years (Wolfe, Dunavon, & Diamond, 2007, Ewald, 1995). Indeed, it has been estimated that parasitic infections have been responsible for more human deaths than all other causes of death put together (Inhorn & Brown, 1990). Parasites therefore imposed powerful selection pressures that shaped the evolution of all animal species—including humans (Fumagalli, Sironi, Pozzoli, Ferrer-Admettla, Pattini, & Nielsen, 2011; Knoll & Carroll, 1999; Zuk, 2007). This has resulted in many adaptations that are so fundamental to human nature that most people take them for granted. These adaptations include the capacity to reproduce sexually rather than asexually (Zuk, 1992) and—more obviously—the physiological mechanisms that comprise humoral and cell-mediated immunological responses to infection. The sophistication of mammalian immune systems (e.g., humans have an immunological capacity to generate billions of unique antibodies; Fanning, Connor, & Wu, 1996; Janeway, 2001) is a testament to the extraordinarily powerful selection pressures imposed by infectious diseases throughout evolutionary history.

But if the existence of the immune system attests to the powerful selection pressures that parasites have imposed on the evolution of mammalian physiology, it also forces us to consider more carefully whether these selection pressures could have led also to the evolution of a "behavioral immune system." It is unlikely that a motivational system facilitating behavioral defense would have evolved if it merely duplicated the adaptive benefits offered by immunological defenses. Is it plausible that, in addition to the adaptive benefits offered by immunological defenses against infection, there would have been further, unique adaptive benefits associated with *behavioral* defenses against infection?

The answer appears to be yes. Although immunological defenses are invaluable at detecting and fighting infections within the body, they also have shortcomings and limitations. Immunological defenses are costly. An immune response to bacterial infection, for example, typically involves an increase in body heat, experienced locally as inflammation or systemically as fever. This response comes at great energetic cost (e.g., it has been estimated that a 13% increase in metabolic activity is required to increase human body temperature by just 1^o Celsius; Dantzer, Kent, Bluth, & Kelley, 1991). Immunological responses not only consume substantial caloric energy—which otherwise could be allocated to sustain other physiological systems—they can also be temporarily debilitating. Many symptoms of infection (such as fever and fatigue) are not direct consequences of infection; they are instead consequences of immunological responses to infection. These consequences temporarily inhibit individual organisms' ability to engage in other forms of fitness-enhancing behavior such as mating and caring for offspring. Finally, another limitation of immunological responses is that they are merely reactive, occurring only *after* infection has already occurred. Parasitic intruders may wreak significant damage during the latency period between the time they enter the body and the time that the immune system mobilizes a defensive response. Because of these nontrivial shortcomings associated with immunological defenses, there would have been unique adaptive value associated with a motivational system that facilitated behavioral avoidance of infection in the first place.

Empirical evidence of anti-parasite behavioral defenses is widespread across the animal kingdom (Cremer, Armitage, & Schmid-Hempel, 2007; Hart, 1990; Meunier, 2015). Some of these behavioral defense strategies are not actually prophylactic strategies, but instead are behavioral responses to existing parasitic infections and promote recovery from those infections (e.g., ingestion of medicinal plants; Huffman, 2001). In addition, many animals also engage in behaviors that adaptively minimize the risk of infection in the first place. Some of these prophylactic behaviors are *reactive* responses to entities within an animal's immediate vicinity—entities that, on the basis of sensory cues, are appraised as representing some immediate risk of infection. For example: lobsters, frogs, and rodents all have means of perceptually identifying other lobsters, frogs, or rodents that are infected with parasites, and actively avoid them (Behringer, Butler, & Shields, 2006; Kavaliers, Choleris, & Pfaff, 2005; Kiesecker, Skelly, Beard, & Preisser, 1999); and chimpanzees ostracize other chimpanzees that exhibit signs of infection (Goodall, 1986). In addition to these reactive behavioral defenses against parasite infection, many animals also engage in more *proactive* defenses: Even under circumstances in which there is no perceptual evidence of infectious entities in the immediate environment, animals engage in actions that manage a latent infection risk, thereby reducing the likelihood that this latent risk becomes manifest in ways that would require reactive avoidance. For example, some species of ants proactively inhibit the presence of bacteria in their immediate environment by lining their nests with antibiotic resins (Chapuisat, Oppliger, Magliano, & Christe, 2007). Similarly, many species of birds and rats proactively minimize exposure to ectoparasites by using specific native leaves or branches as fumigants in their nests (Clark & Mason, 1988; Hemmes, Alvarado, & Hart, 2002).

Humans too employ behavioral strategies that reduce infection risk. Some of these behaviors (e.g., vaccinations, condom use) are deliberative, self-consciously intentional, and informed by recent technological advances in a way that distinguishes them from the behavioral strategies observed in ants and lobsters and frogs and chimpanzees. But other human behavioral tendencies—such as our tendency to avoid touching foul-smelling objects and to avoid affiliating with people with anomalous appearances—more closely mimic the "natural" forms of disease-avoidant behaviors observed in other animals. Some of these latter phenomena have been the focus of psychological inquiry for many years (e.g., Rozin & Fallon, 1987). But only in recent years has the evolved motivational psychology of disease-avoidance—and its wide-ranging implications—become an active focus of theory and research within the psychological sciences.

2.2. Brief History of Disease Avoidance within the Literature on Human Motivation

In his pioneering textbook on social psychology, McDougall (1908) anticipated recent work on the behavioral immune system by making an explicit distinction between “The instinct of flight and the emotion of fear” from “The instinct of repulsion and the emotion of disgust,” but he failed to buttress this distinction with conceptual arguments about the nature of infectious diseases compared to non-disease threats, nor did he marshal any real evidence to support that distinction.

Subsequent to McDougall (1908), the most influential overviews of human motives made no meaningful distinction between infectious diseases and the various other threats to human welfare. Consider, for example, the catalogs of needs identified by Murray (1938) and Maslow (1943)—both of which continue to be featured prominently in contemporary psychology textbooks. Maslow's (1943) model includes a single broad category of needs pertaining to safety, and Murray (1938) identifies a need for "harm avoidance"; but neither make any principled distinction between things that pose different kinds of threats to individuals' safety or that cause different kinds of harm. Consequently, these highly influential models, like most models of motivation within the psychological literature, tacitly treat all threats to physical safety—whether the threat is due to disease, predation, fire, or flood—as motivationally equivalent.

In recent years, however, psychological scientists have attended more closely to the possibility that different kinds of threats may be associated with psychologically distinct response mechanisms. Boyer and Lienard (2006) make a case for a “hazard-precaution system” that governs the detection and appraisal of a broad array of hazards and threats (e.g., predation, contamination, resource scarcity). They also suggest that, following appraisal, reactions to different kinds of hazards are guided by different decision rules—associated with different neural mechanisms—that are unique to the specific hazard at hand. Woody and Szechtman (2011) take a similar approach in describing a “security motivation system” that promotes wariness and vigilance for subtle cues connoting threats to security. They suggest that this security motivation system is sensitive to a wide range of cues that connote different kinds of threats (e.g., unfamiliar noises connoting the threat of predation, morphological anomalies connoting the threat of infection). Once detected, functionally distinct threats such as predation and infection "may be handled by distinguishable, although related, subsystems” (Woody & Szechtman, 2011, p. 1030).

Disease avoidance has been identified as a unique motivational system within several conceptual models that draw explicitly on the logical principles of evolutionary biology. Kenrick and Griskevicius (2013; see also Kenrick et al., 2010) outline a set of evolutionarily fundamental human motives within a structural framework inspired by Maslow's (1954) famous pyramid of needs; within this revised motivational pyramid, disease avoidance is presented as a unique motive that is conceptually distinct from other forms of self-protection. Bernard (2012) too uses an evolutionary conceptual analysis to identify a set of motivational systems that are likely to be functionally distinct and, in doing so, distinguishes between "threat avoidance" and "illness avoidance" as separate motives.

In perhaps the most carefully articulated conceptual model of this sort, Aunger and Curtis (2013) note that, although there is a general fitness-relevant need to minimize the threat posed by biological agents that attack the body, there are important functional differences between agents that attack the body from outside (predators) and those that attack from within (parasites). They suggest that these two functionally distinct kinds of threat constrained the evolution of two distinct motivational systems, which they label according to the different associated emotions: fear and disgust: "First, *fear* drives behavior that avoids hurt-from-without threats, including predators, but also aggressive conspecifics and accidents... Tactics include aggregating in a group, fleeing, hiding, and avoiding environmental dangers such as fires and floods. Second, the *disgust* motive drives the avoidance of hurt-from-within threats. Its task is to cause the avoidance of sick others, 'off' foods, disease vectors, and pathogen contamination" (Aunger & Curtis, 2013, p. 54).

2.3. Unique Functional Implications Associated with the Threat Posed by Parasites

Although Aunger and Curtis (2013) characterize the difference between parasitic threats and other threats as being one of location—outside the body versus inside the body—the functional distinction that matters most is not the location of attack, *per se*. Parasites are functionally distinct from other threats primarily because of the physical characteristic that allows them to enter the body in the first place: They are exceptionally small.

Most other fitness-relevant threats are sizeable enough to be perceived directly, and to be appraised as threats, on the basis of sensory cues that convey size, location, movement and (in the case of many predators and dangerous conspecifics) intent. In contrast, most infectious diseases are caused by organisms that are so tiny as to be functionally invisible (as well as un-hearable, un-smellable, un-tastable, and impalpable). Because they are imperceptible to human sensory systems, their presence can be perceived only indirectly (e.g., the rotting smell of meat that has been consumed by invisible populations of bacteria, or the sickly appearance of a person who has already been imperceptibly infected). Often their presence cannot be perceived at all. The upshot is that, when it comes to the psychological means of appraising the threat that they pose, disease-causing parasites are functionally different from most other threats.

The imperceptibility of parasites also has unique functional implications for behaviors that might mitigate their threat. Larger, directly perceptible threats are associated with logically straightforward, easily teachable and easily learnable behavioral strategies that can be employed to minimize the threat. (The threat of predation can be mitigated with flight, and sometimes fight. The threat of falling off a cliff can be mitigated by staying away from the cliff's edge.) Not so with infectious diseases. Different species of parasites move, and are transmitted from host to host, in a variety of different ways. Until very recently in human history, those means of movement and modes of transmission remained outside the realm of human comprehension. Furthermore, behavioral strategies that are effective in reducing vulnerability to other threats may be useless, or worse, as protection against the transmission of infectious diseases. For example, although aggregating in groups may help provide protection against predatory attacks, grouping behavior provides no protection against the transmission of parasites. Indeed, it can have the opposite effect.

In sum, infectious diseases are functionally distinct from most other threats—in terms of detection and appraisal, and in terms of the behaviors that serve to mitigate the threat. Because of these functional distinctions, it is not only plausible that there evolved a motivational system that responds adaptively to the threat of infectious diseases, it is also plausible that this system is psychologically distinct from other self-protective motives.

2.4. Empirical Evidence of a Psychologically Unique Motivational System

Motivational systems facilitate specific kinds of goal-directed behavior, and these goal-directed actions are often accompanied by specific affective states. The characteristic affective response associated with disease avoidance appears to be disgust—a conceptual connection so tacitly tight that some scientists use the word "disgust" to refer to the motivational system itself (Aunger & Curtis, 2013; Lieberman & Patrick, 2014). The emotional experience of disgust may have evolved from a more ancient and functionally specific distaste response to oral stimuli (Rozin, Haidt, & McCauley, 2000), and many contemporary conceptual accounts identify infectious diseases as the primary selective pressure underlying its evolution (e.g. Curtis, 2007; Oaten, Stevenson, & Case, 2009; Tybur, Lieberman, Kurzban, & DeScoli, 2013).

Supporting this conceptual analysis is evidence that the most subjectively disgusting objects tend to be those that historically posed the greatest threat of disease (Curtis, de Barra, & Aunger, 2011; Oaten et al., 2009). Importantly, the disgust response is distinct from the affective responses elicited by functionally different forms of threat. In one illustrative study (Bradley, Codispotti, Sabatinelli, & Lang, 2001) participants were presented with a 72 pictures and reported the emotions that were evoked when looking at each picture. Included in the stimulus set were pictures connoting potential risk of infection, as well additional pictures connoting other threats to physical well-being (e.g., accidents). In response to pictures connoting infection risk, participants were more likely to report feeling disgust than fear, whereas they reported feeling more fear than disgust in response to pictures connoting other threats.

Research on attention and cognition provide further evidence that people respond in psychologically distinctive ways to infection-connoting stimuli. Compared to stimuli that connote other forms of threat (and which arouse fear), infection-connoting stimuli (which arouse disgust) have been found to exert an especially powerful hold on visual attention (Krusemark & Li, 2011; Van Hooff, Devue, Vieweg, & Theeuwes, 2013). Perceivers also show especially enhanced recall and recognition for disgust-eliciting stimuli—even compared to equally arousing fear-eliciting stimuli—and this distinctive effect on memory persists even when controlling for differences in visual attention (Chapman, Johannes, Poppenk, Moscovitch, & Anderson, 2013).

A large body of physiological evidence also supports the conclusion that the threat of infectious diseases is associated with a motivational response distinct from that associated with other forms of threat. In numerous experiments, individuals have been presented with stimuli connoting either the threat of infection or other forms of threat, and specific physiological responses to those stimuli have been assessed. Several of these studies reveal unique neural responses to infection-connoting stimuli (Baumann & Mattingley, 2012; Stark et al., 2007; Tettamanti et al., 2012; Wright, He, Shapira, Goodman, & Liu, 2004). For example, Stark et al. (2007) presented participants with a variety of images, including some that connoted the risk of infection (e.g. dirty toilets, body products), and others that connoted predatory threats (e.g., physical attacks, weapons). Although some brain regions (the amygdala and the occipital and prefrontal cortices) showed increased activation in response to both infection- and predation-relevant images, other brain regions were uniquely activated in response to these different forms of threat: Predatory threat was uniquely associated with activation in the middle temporal cortex and medial parietal structures, whereas the risk of infection was uniquely associated with activation in the insula, inferior temporal gyrus, and fusiform gyrus.

The perceived threat of infection—and its associated emotional response of disgust—is also associated with a unique pattern of autonomic nervous system responses (Kreibig, 2010; Mauss & Robinson, 2009). Kreibig (2010) reviewed evidence from 134 experiments assessing a variety of cardiovascular, respiratory, and electrodermal indicators of autonomic activation following presentation of emotion-eliciting stimuli, including stimuli connoting the risk of infection. Results revealed that these disgust-eliciting stimuli were associated with a pattern of autonomic activity "characterized by sympathetic–parasympathetic co-activation and faster breathing, particularly decreased inspiration" (Kreibig, 2010, p. 403). This pattern is indicated by changes on many specific cardiovascular variables (heart rate acceleration, increased heart rate variability, increased total peripheral resistance, increased systolic and diastolic blood pressure, increased finger pulse amplitude, decreased stroke volume, decreased cardiac output), as well as on several respiratory and electrodermal variables (increased respiration rate, decreased inspiratory time, decreased respiratory volume, increased skin conductance response and skin conductance level). This pattern of responses is distinct in multiple ways from the pattern of autonomic responses elicited by other kinds of threat-connoting stimuli. For instance, whereas other threatening stimuli (of the sort that arouse fear) are associated with increased cardiac output, decreased heart rate variability, and decreased total peripheral resistance, infection-connoting stimuli are uniquely associated with *decreased* cardiac output, *increased* heart rate variability, and *increased* total peripheral resistance.

In sum, not only is there a compelling conceptual argument that there evolved a functionally unique motivational system facilitating behavioral defense against disease-causing parasites, there is empirical evidence that this motivational system—the behavioral immune system—is psychologically distinct from other avoidance-oriented motives that govern human behavior.

3. Two Underlying Principles with Implications for Social Psychological Phenomena

Even if such a motivational system exists, and even if its activation is associated with predictable psychological phenomena, this is no guarantee that it has implications for *social* psychological phenomena. After all, there is an evolutionary ancient motivational system underlying the experience of thirst and the desire to ingest liquids, but there is no meaningful psychological literature linking this motivational system to social cognition or social behavior. In contrast, the behavioral immune system does have straightforward implications for social psychological phenomena. For instance: Because the behavioral immune system leads people to respond aversively to infectious things, then it is likely to produce aversive responses to specific people who are infectious. The obvious social psychological implication is stigmatization of people who are, in fact, suffering from infectious diseases (Crandall & Moriarty, 1995; Kurzban & Leary, 2001).

Still, even if a motivational system has some obvious implications for highly specific social psychological phenomena, this is does not guarantee that it has non-obvious or otherwise interesting implications across a *wide range* of social psychological phenomena. Nor does it guarantee that these implications can be integrated into the paradigmatic *situationist* theme of social psychology, which emphasizes the many ways in which social psychological phenomena vary depending on the specific situations and circumstances that people are in. The behavioral immune system does have non-obvious implications for a wide range of social psychological phenomena—including implications for attitudes toward people who are *not* infectious, and for other responses (such as conformity to majority opinion) that might superficially appear to have nothing whatsoever to do with infectious diseases. And these implications do indeed vary depending on the specific situations that people are in.

Underlying these social psychological implications are two key principles that govern exactly how the behavioral immune system actually works. Both principles emerge from the logic of a cost-benefit analysis.

3.1. The Smoke Detector Principle

Although it was evolutionarily "designed" to govern responses to stimuli that pose some risk of infection, the behavioral immune system also governs responses to many stimuli—including people—who pose no objectively meaningful risk of infection at all.

The reasons for this overgeneralized response result from the fact that the behavioral immune system responds not to the objective risk of infection, but rather to the *inferred* risk of infection as indicated by superficial cues—perhaps especially the kinds of salient sensory cues that historically have been associated with infectious diseases (e.g., facial anomalies and skin discolorations). Many of these cues may be probabilistically predictive of the actual infection risk, but even highly diagnostic cues are imperfect. This results in a signal-detection problem, with the inevitable consequence that perceivers will sometimes respond to objectively benign stimuli as though they truly indicated an infection risk—especially when those objectively benign stimuli perceptually mimic truly problematic stimuli.

This overgeneralization is not simply a product of random signal detection error; it is also the product of cognitive mechanisms that evolved to adaptively manage the fitness implications associated with different kinds of signal detection errors (Haselton & Nettle, 2006; Haselton, Nettle, & Murray, 2015). When perceivers use superficial cues to infer infection risk, two kinds of errors are possible: (a) inferring the presence of an infection risk when, in fact, there is no such risk (a false positive error); and (b) inferring the absence of infection risk when, in fact, there is a real risk of infection (a false negative error). These errors are equally erroneous but unequally costly. False positive errors imply objectively unnecessary avoidance of benign entities, which is unlikely to lead to particularly costly consequences. False negative errors imply unsuspecting contact with actually infectious entities, which could potentially have very costly consequences for health and fitness. Given these unequal costs, the appraisal of infection risk is likely to be biased in a predictable manner consistent with a "smoke detector principle" (Nesse, 2005) that applies to cue-based appraisal of dangers more generally.

The smoke detector principle gets its nickname from a design feature of the smoke detectors that you find on the ceilings of many homes. Smoke detectors are designed to serve a straightforward function: to provide an audible alarm in the event of a house fire. But they do not detect fire directly; instead, they detect airborne particles of the sort associated with smoke. Two kinds of smoke detection errors are possible, and these errors differ hugely in their costs. A false positive error (sounding an alarm in response to benign bit of cooking smoke) is irritating. A false negative error (failing to sound an alarm in the presence of an actual house fire) is potentially catastrophic. Given these differences in costs, most people willingly put up with lots and lots of temporarily irritating false positive errors in order to avoid even one potentially fatal false negative error. Smoke detectors are calibrated accordingly: In order to minimize the likelihood of a catastrophic false negative error, they are extraordinarily sensitive to any usual concentration of airborne particulates. The inevitable consequence is that they make lots of false positive errors—responding to over-toasted bagels and pan-seared steaks in exactly the same way that they would to an actual house fire.

Analogously, the behavioral immune system is highly sensitive to broad categories of cues that imperfectly connote potential infection risk. This hypersensitivity minimizes the likelihood of making a false negative error—of failing to respond to entities or actions that really do pose an infection risk. As an inevitable consequence of this hypersensitivity, the behavioral immune is prone to make lots of false positive errors instead, responding to objectively benign entities and actions in the same way that it would to things that pose a real infection risk.

For example: Just as people respond with disgust and behavioral avoidance to the perception of feces, they also respond with disgust and behavioral avoidance to objectively harmless chocolate fudge that just happens to be sculpted into the shape of feces (Rozin, Millman, & Nemeroff, 1986). And—to anticipate some of the implications for social psychological phenomena that we review in greater detail below—just as people respond with disgust and behavioral avoidance to individuals who actually are suffering from an infectious disease, they also respond with disgust and behavioral avoidance to individuals who merely have superficial facial disfigurements (Ryan, Oaten, Stevenson, & Case, 2012).

3.2. The Functional Flexibility Principle

The existence of the behavioral immune system is predicated in part upon the fact that immunological defenses against parasites are costly, and that the prophylactic avoidance of infection obviates the need to deploy these costly immunological defenses. But, just as immunological responses to infection have costs as well as benefits, so too do prophylactic behavioral responses. Behavioral avoidance of infection risk consumes both caloric and cognitive resources. These resources might otherwise be allocated to other fitness-relevant activities. In contemporary human populations characterized by an abundance of both caloric and cognitive resources, these costs might seem inconsequential. But throughout much of human evolutionary history, both caloric and cognitive resources were less abundant, and so this cost/benefit problem was nontrivial.

This same kind of cost/benefit problem applies to many aspects of evolved cognition—including motivational systems that facilitate avoidance of other kinds of dangers as well as other motivational systems that facilitate the formation of interpersonal bonds, mating behavior, and other approach-oriented actions. Across all these motivational domains, the cost/benefit problem appears to have been substantially solved by the evolution of mechanisms that allow the motivational system to respond flexibly, in a manner that is informed by context-specific information conveying the extent to which the functional benefits of these responses might outweigh their associated costs.

When applied to the behavioral immune system, this "functional flexibility principle" (Schaller, Park, & Kenrick, 2007; Schaller & Neuberg, 2012) has straightforward implications: When contextual cues imply that perceivers are relatively invulnerable to infection, the system produces relatively muted responses. In contrast, when contextual cues imply that perceivers are more vulnerable to infection, the system produces stronger affective, cognitive, and behavioral responses. An illustrative example is provided by research on pregnancy and the experience of disgust. Immunological responses to infection are suppressed in the first few weeks of pregnancy and, as a consequence, women in that early stage of pregnancy are more vulnerable to infection. As a further consequence, women in that same early stage of pregnancy are (compared to women in later stages of pregnancy) more likely to exhibit relatively intense disgust responses to stimuli that, on the basis of superficial cues, appear to pose some risk of infection (Fessler, 2002; Fessler, Eng, & Navarette, 2005; Flaxman & Sherman, 2000).

This functional flexibility principle applies not only to affective responses, but also to a wide range of phenomena pertaining to social cognition and social behavior. To the extent that specific social attitudes and interpersonal actions are influenced by the behavioral immune system, these attitudes and actions are especially likely to be expressed in situations in which people are—or subjectively perceive themselves to be—more vulnerable to infection. For this reason, many relevant empirical investigations have employed research methods that either measure or experimentally manipulate the extent to which individuals perceive themselves to be vulnerable to infectious diseases, and test the extent to which these variables predict outcomes of social psychological interest.

4. Implications for Specific Social Psychological Phenomena

Drawing on the guiding principles reviewed above, dozens of empirical investigations document specific ways in which activation of the behavioral immune system has implications for social cognition, social attitudes, and interpersonal behavior. In this section, we provide a summary overview of this body of evidence, and highlight key conclusions.

4.1. Selective Attention to Anomalous Faces

Because many infectious diseases are spread through interpersonal contact, social interactions are associated with the risk of disease transmission. These interactions have many potential benefits too, of course. In order to maximize the potential benefits and minimize the potential costs of social interaction, perceivers must perceptually discriminate between individuals who do and do not pose an infection risk. Therefore, superficial physical features that identify individuals as potential infection risks are likely to capture and hold perceivers' visual attention—and to do so especially under circumstances in which perceivers feel especially vulnerable to infection.

One test of this hypothesis was reported by Ackerman et al. (2009). Participants completed a computer-based "dot probe" task that assessed the time it took for visual attention to shift from an initial visual stimulus to a new stimulus elsewhere on a computer screen. The initial visual stimuli were individual human faces. The tendency for faces to hold perceivers' visual attention was indicated by slower response times to the novel stimuli (which were simple geometric shapes). Importantly, some of the faces were "normal," whereas others were characterized by superficial disfigurements—visual cues that, in accordance with the smoke detector principle, tend to heuristically connote an infection risk. Results on this task therefore tested whether visual attention was held especially strongly by disfigured faces. The procedures also included an additional experimental manipulation: Prior to the visual attention task, participants watched one of two brief slide shows—one of which depicted images and text related to architecture, whereas the other depicted images and text related to infectious diseases and the ease with which they are transmitted.

Results revealed that (consistent with the logical implications of the smoke detector principle) perceivers were slower to disengage visual attention from disfigured faces, compared to "normal" faces. Results also showed that (consistent with the logical implications of the functional flexibility principle), this attentional bias was especially pronounced under conditions in which the threat posed by infectious diseases was especially salient.

It is worth noting that Ackerman et al. (2009) also reported an additional experiment, designed to test whether the increased attention to disfigured faces manifested also in increased recognition accuracy for those faces. It did not. If anything, the reverse was true: People made more recognition errors when attempting to discriminate between previously-seen and –unseen disfigured faces than when attempting to discriminate between previously-seen and –unseen "normal" faces. Thus, although people may devote more visual attention to individuals who superficially appear to pose an infection risk, they do not appear to be encoding much in the way of actual individuating information about them.

4.2. Stigma and Prejudice

The avoidance of infection depends not merely on perceivers' capacity to perceptually identify people who pose an infection risk; it depends more directly on their capacity to avoid contact with those people. The implication is that perceivers are likely to stigmatize individuals displaying cues that connote some sort of infection risk. This stigmatization—and the set of prejudicial responses associated with it—is especially likely to emerge under conditions in which perceivers feel especially vulnerable to infection.

There is now a substantial body of literature indicating that the behavioral immune system does indeed have unique implications for the psychology of stigma and prejudice (Oaten, Stevenson, & Case, 2011; Schaller & Neuberg, 2012). The most obvious implication pertains to prejudices against people who actually are diseased (Kurzban & Leary, 2001). One illustrative experiment showed that people generally prefer to maintain greater physical distance from others who are perceived to be suffering from some sort of illness, and this is especially the case when the illness is perceived to be more highly contagious (Crandall & Moriarty, 1995).

The implications for prejudice are not limited just to prejudice against individuals who actually are diseased. Much additional research reveals that the behavioral immune system also contributes to prejudices against many individuals who pose no infection risk whatsoever, but are instead characterized by perceptual anomalies in facial and/or body morphology (cues that historically have been correlated with infection and that—consistent with the smoke detector principle—trigger an underlying cue-detection system that is hypersensitive and prone to false alarms). In fact, given the evolutionary antiquity of the underlying mechanisms, the behavioral immune system may produce highly automatic negative responses to perceptually salient (but potentially misleading) morphological anomalies, and may do so even more strongly than it does to more accurate (but abstract) language-based declarative knowledge about a person's health status. In one illustrative study (Duncan, 2005), participants were provided with photographs and brief biographical sketches of two men. One man had a port wine stain birthmark on his face, but this birthmark was described as superficial and the man was described as healthy. The other man looked "normal" but was described as being infected with tuberculosis. Participants then responded to a reaction-time task (a version of the implicit association test) that assessed which of the two men was more strongly associated with the semantic concept "disease." Results showed that "disease" was implicitly associated with the facially disfigured man (who was known to be healthy) even more strongly than it was with the man who was actually known to be diseased.

Additional research has applied the functional flexibility principle to these kinds of prejudices, and shows that prejudices against various categories of morphologically anomalous people—including elderly people, obese people, and people with physical disabilities—are amplified under conditions in which perceivers feel more vulnerable to infection (Duncan & Schaller, 2009; Park, Faulkner, & Schaller, 2003; Park, Schaller, & Crandall, 2007). For example, Park et al. (2007) assessed the extent to which the semantic concept "disease" was implicitly associated with obese individuals to a greater extent than with normal-weight individuals. Prior to the assessment of this prejudicial cognitive association, participants watched a brief slide show that made temporarily salient either the threat posed by infectious diseases or (in a control condition) the threat posed by potentially fatal accidents. Results revealed that, even compared to the accidents-salient condition, the diseases-salient condition led to exaggerated prejudicial cognitions about obese people. Thus there appears to something psychologically unique about the specific threat posed by infectious diseases that contributes to anti-fat prejudice. Additional results revealed that these effects of disease-threat were independent of other psychological variables that contribute to anti-fat prejudice.

In addition to its implications for prejudices against people who look superficially anomalous, the behavioral immune system also has implications for prejudices against outgroups, especially outgroups that are perceived to be subjectively "foreign." There are several reasons why. One reason is that foreign peoples may have physical appearances that are subjectively perceived to be anomalous (and so may trigger the behavioral immune system for the same reason that disfigured or obese people do). A second reason is that contact with exotic peoples may increase the risk of exposure to exotic parasites that pose an especially potent threat to immunological defenses. (Adaptive immunity is highly localized; even adjacent villages can have highly variable immune defenses to specific strains of parasites; Miller et al., 2007.) A third reason is that cultural outsiders may be ignorant of—and more likely to violate—local rituals and norms that serve as barriers against disease transmission (e.g., local practices pertaining to hygiene, food preparation, etc.). The implication is that foreign peoples may be implicitly perceived as posing an infection risk and this risk may be perceived to be especially strong under conditions in which perceivers feel especially vulnerable to infection. Ethnocentric and xenophobic responses may be expressed accordingly.

Empirical research supports these implications. Just as women in the early stages of pregnancy (in which their immunological defenses are naturally suppressed) are especially easily disgusted, they also report especially strong ethnocentric and xenophobic attitudes (Navarrete, Fessler, & Eng, 2007). These amplified responses were accounted for by increases in negative general affect. Additional studies reveal that the effects of disease threat on xenophobia are unique, and distinct from the effects of other threats that also contribute to xenophobia (Faulkner, Schaller, Park, & Duncan, 2004; Schaller & Neuberg, 2012). In one experiment reported by Faulkner et al. (2004), Canadian participants completed a task that assessed the extent to which they favored immigrants from familiar countries compared to immigrants from more subjectively foreign countries. Prior to assessing these xenophobic attitudes, participants watched a slide show that either made the threat posed by infectious diseases salient or (in a control condition) made the threat posed by accidents salient. Results revealed that, even compared to the accidents-salient condition, the diseases-salient condition led to exaggerated levels of xenophobia (see Figure 1).

These findings are complemented by correlational results showing that people who are most dispositionally concerned about infectious diseases (i.e., people who, regardless of their actual susceptibility to infection, subjectively perceive themselves to be more vulnerable), or who are especially prone to disgust, are also especially prejudiced against people who are perceived, heuristically, to pose a higher risk of infection—including homosexuals, people who appear morphologically anomalous, and members of subjectively foreign outgroups (Faulkner et al., 2004; Hodson & Costello, 2007; Inbar, Pizarro, Knobe, & Bloom, 2009; Lieberman, Tybur, & Latner, 2012; Navarette & Fessler, 2006; Olatunji, Haidt, McKay, & David, 2008; Park et al., 2003; Terrizzi, Shook, & Ventis, 2010; Vartanian, 2010).

Also informative are several studies that measured prejudicial responses following procedures designed to make perceivers feel relatively *in*vulnerable to infection (Huang, Sedlovskaya, Ackerman, & Bargh, 2011). One experiment showed that, among people who subjectively perceived themselves to be vulnerable to disease, the tendency to be prejudiced (against various categories of people who are heuristically perceived to pose an infection risk) was reduced following a procedure in which they disinfected their hands with an anti-bacterial wipe. Additional studies showed that the typical relation between subjective perceptions of disease-vulnerability and prejudice was reduced if individuals had recently been inoculated against influenza and were explicitly informed that the inoculation reduced their vulnerability to infection. These results further support a unique link between the behavioral immune system and the psychology of prejudice, and have useful implications for the development of interventions that might reduce prejudice (for additional discussion of prejudice-reduction implications, see Schaller & Neuberg, 2012).

4.3. Social Categorization

In addition to the many studies that link the behavioral immune system to prejudices against people who belong to specific kinds of social categories, additional lines of research document its implications for additional cognitive biases pertaining to the perception of social categories.

One set of results suggests that when the behavioral immune system is activated, people perceive greater dissimilarity between ingroups and outgroups. This conclusion emerges from two studies that focused on the perceived degree of similarity between the speech sounds of people who, because of their accents, were categorized as either ingroup or outgroup members (Reid, Zhang, Anderson, Gasiorek, Bonilla, & Peinado, 2012). Results revealed that people who were more chronically disgusted by pathogens perceived greater dissimilarity between ingroup and outgroup accents, and this effect was especially pronounced under conditions in which the risk of infection had been made temporarily salient. These effects were specific to pathogen disgust (perceptions of similarity were not predicted by individuals' tendency to be disgusted by unusual sexual acts nor by moral violations), and also specific to the threat posed by infectious diseases (no such effect emerged in a control condition in which the threat posed by gun violence was made salient).

Other studies reveal implications for biased judgments about whether individuals belong to specific social categories (Makhanova, Miller, & Maner, 2015; Miller & Maner, 2012). Across two studies that used a minimal groups paradigm to create ad-hoc ingroups and outgroups, Makhanova et al. (2015) found that participants who felt especially vulnerable to disease (either as a chronic trait, or temporarily as the result of an experimental procedure that temporarily made salient the threat of an H1N1 flu pandemic) were especially likely to categorize individuals displaying disease-connoting cues (e.g., facial anomalies associated with old age) as an outgroup member rather than an ingroup member. A different categorization bias was documented by Miller and Maner (2012). In a correlational study, they found that individuals who were chronically concerned about infection were especially likely to show a bias toward including average-weight individuals in the category "obese." Three additional experiments employed experimental manipulations to make disease threat temporarily salient and, in all cases, produced conceptually similar results: When the threat of infection was especially salient, individuals showed an exaggerated tendency to categorize ambiguous target persons as being members of disease-connoting social categories. All three experiments included a control condition in which other threats (e.g., potentially fatal accidents) were salient; and, in all experiments, the social categorization bias was specific to the threat of infection.

4.4. Interpersonal Attraction

Inferences about facial attractiveness are based on a variety of morphological features—including bilateral symmetry and prototypicality—that may correlate with heath status; consequently, the subjective appraisal of facial (un)attractiveness may itself serve as a cue indicating whether a person does or does not pose an infection risk (Zebrowitz & Montepare, 2006; Weeden & Sabini, 2005). The implication is that, although many other psychological motives and mechanisms also contribute to the common attitudinal preference for subjectively attractive faces (compared to unattractive faces), this preference may be partially attributable to the behavioral immune system. If so, then the magnitude of these face preferences is likely to vary depending on the extent to which perceivers feel vulnerable to infection. Several studies have produced evidence supporting this hypothesis.

Some of these studies focus on overall subjective assessments of facial attractiveness. Park, van Leeuwen, and Stephen (2012) report results from three correlational studies, all of which showed that relatively unattractive faces were judged to be especially unattractive by individuals who are more highly disgusted by pathogens. This relationship was specific to pathogen disgust (no effects were found for individuals' tendency to be disgusted by sexual acts or by moral violations).

Additional studies have focused specifically on preferences for symmetrical (compared to asymmetrical) faces. In a correlational study, Young, Sacco, and Hugenberg (2011) found that individuals who chronically feel more subjectively vulnerable to infection showed a stronger preference for symmetrical faces. More convincingly, Young et al. (2011) also conducted an experiment that manipulated the salience of either the threat of infection or a different threat. Compared to the control threat, when the threat of infection was salient, perceivers showed an exaggerated preference for symmetrical faces (see Figure 2). It is notable that this effect was not only specific to the threat of disease, it was also specific to the perception of faces (no effect of the manipulation emerged on preferences for symmetrical non-social stimuli).

In addition to serving as a perceptual cue indicating an individual's own health status, symmetry may also be diagnostic of an individuals' potential to produce offspring of high genetic quality (Tybur & Gangestad, 2011). This suggests that the preference for symmetrical faces may be especially pronounced in mating contexts. Moreover, because offspring with higher genetic quality are more likely to have stronger immune systems—and thus to be more resistant to infectious diseases—the preference for mates with symmetrical faces may be especially great under conditions that connote increased infection risk. Several results support this hypothesis. In rural Bangladesh (an ecological context characterized by a generally high prevalence of infectious diseases), individuals who suffered more illnesses during childhood showed stronger preferences for attractive faces during adulthood, and this effect was specific to opposite-sex faces (de Barra, DeBruine, Jones, Mahmud, & Curtis, 2013). Analogously, results from a laboratory experiment in the U.K. showed that, compared to a no-threat control condition, when the threat of infection was made temporarily salient, people consequently showed increased preference for facial symmetry when perceiving opposite-sex faces, but not same-sex faces (Little, DeBruine, & Jones, 2011).

Among men, facial cues of masculinity (e.g., a pronounced brow ridge) may also serve as signals indicating strong immune function, as well as the capacity to produce offspring with strong immune systems (Tybur & Gangestad, 2011). The implication is that a female preference for facial masculinity may also be exaggerated when perceivers feel more vulnerable to infection, and that this effect may be specific to the perception of opposite-sex faces. The experiment by Little et al. (2011) produced results supporting this hypothesis. Another study tested the hypothesis with correlational methods and found that women's preference for more masculine male faces was positively correlated with the tendency to be disgusted by pathogens (Debruine, Jones, Tybur, Lieberman, & Griskevicius, 2010). This relation was unique to pathogen disgust (no such effect was found for sexual disgust or moral disgust).

4.5. Sexual Attitudes and Sexual Behavior

Sexual activity involves close interpersonal contact that brings with it an increased risk of disease transmission. Consequently, just as the arousal of a mating motive can lead people to be less disgusted by sexual acts that typically elicit disgust (Stevenson, Case, & Oaten, 2011), the activation of the behavioral immune system may lead people to be more behaviorally cautious in the context of sexual relationships. One manifestation of this behavioral caution was documented in a study that employed the ambient odor of human feces to activate the behavioral immune system, and then assessed individuals' intentions to purchase and use condoms (Tybur, Bryan, Magnan, & Caldwell-Hooper, 2011). Results revealed that, compared to a no-odor control condition, the disgust-eliciting olfactory cue led to increased intentions to use condoms.

Other studies reveal that individuals who chronically feel more subjectively vulnerable to infectious diseases report a less promiscuous pattern of sexual behavior (Duncan, Schaller, & Park, 2009), and that, among women, this effect emerges most strongly when contextual cues make the threat of infectious diseases temporarily salient (Murray, Jones, & Schaller 2013). The latter study included a control condition that made the threat of violent harm temporarily salient, and this control threat had no discernable impact on inclinations towards promiscuous sexual behavior. The implication is that activation of the behavioral immune system has psychologically unique implications for the inhibition of sexual behavior.

A more recent set of studies identified a rather different and more subtle phenomenon linking disease threat to women's sexual attitudes. Based on the premise (which is well-supported in the biological literature) that female reproductive fitness may be enhanced by the production of genetically diverse offspring, and that this long-term fitness benefit may occur especially within ecologies characterized by high densities of pathogens, Hill, Prokosch, and DelPriore (2015) predicted that when women anticipate a long-term future characterized by increased threats from a variety of diseases, they will consequently desire greater variety in future sexual partners. Hill et al. reported results from five studies that supported this hypothesis. Relative to control conditions (e.g., a condition that made salient a forecast for future economic hardships), women reporting an increased desire for sexual variety under conditions that made salient a forecast for increasing threats from multiple diseases. These effects occurred primarily among women who subjectively perceived themselves to be especially likely to contract infections. These effects did not generalize to preferences for variety in non-sexual domains, and the effects were specific to female sexual attitudes (no such effects were found for men).

Considered together, these various studies suggest a variety of distinct phenomena linking disease threat to sexual attitudes, and further suggest that the nature of these relationships may depend crucially upon whether people—perhaps women especially—are responding to concerns about the immediate threat of infection (of the sort that often arouses disgust), or to a more future-oriented concern with implications for offspring health and fitness.

4.6. Social gregariousness

Social interaction need not be sexual in order to expose individuals to a higher risk of infection. People who are simply more socially gregarious—and thus are likely to come into contact with a greater number of people—are more susceptible to disease transmission (Nettle, 2005). The arousal of the behavioral immune system may therefore be expected to inhibit gregarious social interaction.

There is some evidence consistent with this hypothesis. Some of the evidence is merely correlational: Individuals who are more chronically concerned with disease-avoidance also score lower on measures of dispositional extraversion (Duncan et al., 2009). More inferentially compelling are results from two studies that employed experimental manipulations designed to temporarily activate the behavioral immune system (Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010). Compared to a no-threat control condition, after participants were exposed to information that made the threat of infectious diseases highly salient, they reported lower levels of dispositional extroversion, and also demonstrated stronger avoidant-oriented (and weaker approach-oriented) motor movements in response to social stimuli. These effects were especially pronounced among individuals who were more subjectively worried about their personal vulnerability to infectious diseases.

Neither of these experiments included control conditions designed to make other threats salient, so it remains unclear whether these effects on social gregariousness are unique to the threat posed by infectious diseases. Nonetheless, these results do offer evidence that, when the behavioral immune system is activated, it not only causes people to be more discriminating in terms of who they prefer to have social contact with (as revealed by research on prejudice and attraction, summarized above), it also causes people to be less sociable in general.

4.7. Social Influence

Because of the imperceptibility of parasites, it is only very recently in human history that people acquired a meaningful understanding of the true causes of infectious diseases and, consequently, developed modern methods of combating the threat that they pose (e.g., antibiotics, immunization, public health infrastructure). Prior to these modern technological advances, the primary means of mitigating infection risk depended substantially on adherence to local rituals and other cultural norms. Indeed anthropological research indicates that the majority of behavioral norms in pre-industrial societies functioned as “prescriptions to avoid illness” (Fabrega, 1997, p. 36). Although some of these normative prescriptions may have emerged simply as superstitions with no demonstrable effects on disease transmission, others are likely to have been truly beneficial as buffers against the transmission of infectious diseases (e.g., normative practices in domains of food preparation, personal hygiene, and sexual interaction). Violation of these norms would have increased the risk of infection—not only for the norm violators themselves, but also for others within the local community. Therefore, throughout much of human history, individuals’ conformity to these norms is likely to have served as important means of limiting infection risk.

Conformity can have costs too (e.g., the inhibition of potentially beneficial technological innovations). The disease-buffering benefits of conformity are more likely to outweigh these costs under conditions in which the likelihood of infection is higher. Therefore, based on the functional flexibility principle, individuals’ tendency to express conformist attitudes, and to engage in conformity behavior, is likely to be influenced by subjective assessments of this likelihood. Under conditions in which people feel especially vulnerable to infectious diseases, they are likely to express especially conformist attitudes and to be especially likely to conform to perceived social norms.

These hypothesized implications are supported by results obtained through both correlational and experimental methods (Murray & Schaller, 2012; Wu & Chang, 2012). For instance, Murray and Schaller (2012) found that individuals who felt more subjectively vulnerable to infectious diseases also tended to agree more strongly with statements endorsing conformity to social norms (e.g., “Breaking social norms can have harmful, unintended consequences”), expressed greater liking for people described as having traits that connoted a dispositional tendency to conform (e.g., traits such as “conventional” and “traditional”), and—when evaluating a variety of traits that children might be encouraged to possess—placed a higher value on the trait “obedient.” These relations generally persisted even when statistically controlling for individual differences in perceived vulnerability to other kinds of threat. In addition, both Murray and Schaller (2012) and Wu and Chang (2012) conducted experiments that employed experimental manipulations designed to make temporarily salient the threat posed by infectious diseases. Results revealed more highly conformist attitudes under disease-threat conditions compared to control conditions.

These effects were found not only on the endorsement of conformist attitudes, they also were found on participants' own behavioral conformity to perceived majority opinion. For example, in the experiment reported by Murray and Schaller (2012), a sample of university students were told that their university was considering changing the numerical scale on which course grades are reported on student transcripts, and were asked to indicate their opinion regarding this change. They did so by placing a penny (which the experimenter provided) in one of two clear plastic cups, labeled "Agree" or "Disagree." One of these cups (counterbalanced across conditions) contained 3 pennies already, whereas the other contained 25 pennies—implying a substantial majority opinion expressed by previous student participants. This methodology created the possibility that each participant's own expressed opinion might be influenced by the apparent majority opinion. And, across all participants, it allowed the opportunity to test whether this susceptibility to social influence was greater under conditions in which the threat posed by infectious diseases had been made temporarily salient. It was. (See Figure 3.) When disease-threat was salient, 67% of participants indicated a response that was identical to the apparent majority opinion. This percentage was not only higher than in a no-threat control condition (42%), it was also higher than in another control condition in which a different—but equally anxiety-provoking—threat was salient (53%).

Thus, although perceived threats of other kinds have also been shown to influence conformist attitudes and behaviors (e.g., Griskevicius et al., 2006), the threat posed by infectious diseases has an independent impact. The broader implication is that the behavioral immune system may have psychologically unique implications for susceptibility to social influence.

4.8. Moral Judgment

If activation of the behavioral immune system leads people to be more attitudinally inclined toward conformity, then its activation may also lead people to respond more harshly to others who fail to conform to social norms. This has straightforward implications for the experience of moral outrage and the expression of moral judgments.

This line of reasoning provides a functional framework within which to locate empirical results linking the emotional experience of disgust to moral judgments (e.g., Chapman & Anderson, 2013; Haidt, 2001; Pizarro, Inbar, & Helion, 2011; Rozin, Haidt, & Fincher, 2009). Correlational evidence shows that individuals who are chronically more likely to experience disgust also judge norm violations more harshly (e.g., Jones & Fitness, 2008). This correlation is complemented by experimental evidence showing that when individuals are presented with disgust-eliciting stimuli, they subsequently judge norm violations to be more morally wrong (e.g., Erskine, Kacinik, & Prinz, 2011; Schnall, Haidt, Clore, & Jordan, 2008; Wheatley & Haidt, 2005).

Particularly notable are a set of studies reported by Horberg, Oveis, Keltner, and Cohen (2009). Horberg et al. found that individuals who were chronically prone to experience disgust also more strongly condemned violations of purity norms, but not justice norms. Importantly, this study also assessed individual differences in the tendency to experience anger and fear—emotions associated with conceptually different harm-avoidant goal states. Although dispositional anger predicted moral judgments in the justice domain, it did not predict moral judgments in the purity domain, and the predictive effect of disgust predicted moral judgments in the purity domain even when controlling for anger and fear. In a conceptually complementary experiment, Horberg et al. (2009) induced disgust through a manipulation that made highly salient a means through which many infectious diseases can be transmitted (direct contact with others' feces) and found that, compared to a control condition (in which sadness was induced), the disgusted individuals more strongly condemned actions that violated norms in the domain of moral purity, but not those that violated norms in the domain of physical harm. Together these results show that the arousal of disgust—which serves as an emotion signal of immediate infection risk—has effects on moral judgments that are unique and distinct from effects associated with other negative emotions (including negative emotions that signal the presence of functionally distinct kinds of threat).

The results reported by Horberg et al. (2009) suggest that activation of the behavioral immune system is likely to facilitate especially harsh moral judgments of norm violations when those norms offer the most immediate and obvious protection against disease transmission. Murray and Schaller (2012) report additional results that support this hypothesis. Participants were presented with brief scenarios describing a variety of specific norm violations. Some of these transgression occurred in domains—such as food preparation, personal hygiene, and sexual relations—with clear implications for disease transmission (e.g., "A chef in a restaurant fails to wash his hands after using the bathroom"), whereas others occurred in other domains (e.g., "A car mechanic installs a car part that he knows might be unsafe.") Results showed that, even when controlling for chronic concerns about dangers of other kinds, chronic concern with infection predicted especially harsh judgments of the former category of norm violations compared to the latter category. These results were complemented by the effects of an experimental manipulation: Compared to control conditions, when the threat of infection was temporarily salient, people tended to be especially harsh when judging the moral offensiveness of norm violations that had clear implications for disease transmission.

4.9. Political Attitudes

The behavioral immune system also has implications for political attitudes—especially the endorsement of conservative political attitudes. In the realm of politics and governance, conservatism is typically defined as an ideology that emphasizes maintenance of and conformity to traditional social norms (Altemeyer, 1988; Jost, Glaser, Kruglanski, & Sulloway, 2003; Morris, 1976). Therefore, just as activation of the behavioral immune system has consequences for conformity and moral judgment, it also is likely to be associated with stronger endorsement of conservative political attitudes.

There is now a substantial body of literature that tests, and supports, this hypothesis (for a review, see Terrizzi, Shook, & McDaniel, 2013). Most of these studies are correlational, and most focus not directly on perceptions of infection risk, but instead on individual differences in the tendency to experience the emotion—disgust—associated with infection risk. Results show that individuals who are more prone to experience disgust are also more likely to express attitudes reflecting political conservatism (e.g., Brenner & Inbar, 2015; Inbar, Pizarro, & Bloom, 2009; Olatunji, Tolin, Huppert, & Lohr, 2005; Smith, Oxley, Hibbing, Alford, & Hibbing, 2011; Terrizzi, Shook, & Ventis, 2010, 2012). For example, across a set of studies conducted in the Netherlands, Brenner and Inbar (2015) found that people who were more prone to experience disgust—and to experience disgust in contamination-relevant contexts in particular—reported greater endorsement of attitudes representing conservative political interests (e.g., "It should be impossible to build new mosques in the Netherlands," "Gay couples shouldn't have the same rights in marriage as straight couples," "The EU should interfere less in our political decisions").

Several of these correlational studies attempted to differentiate infection-relevant disgust responses from disgust responses to other kinds of elicitors (e.g., non-normative sexual acts, moral violations). Some studies found no evidence that political conservatism was associated uniquely with infection-relevant disgust (Tybur, Inbar, Güler, & Molho, 2015; Tybur, Merriman, Hooper, McDonald, & Navarette, 2010). Another study—which employed an unusually large and varied sample (*N* = 31,045)—did find that the relation between disgust sensitivity and political conservatism was driven primarily by the tendency to be disgusted specifically by stimuli that connote risk of infection (Inbar, Pizarro, Iyer, & Haidt, 2012).

Given the inferential limitations of these correlational studies, perhaps the most persuasive evidence linking activation of the behavioral immune system to political attitudes comes from an experiment conducted by Helzer and Pizarro (2011). In this experiment, American participants completed a measure of political attitudes in the hallway of a public building. Participants did so either in a control location or in immediate proximity to an anti-bacterial hand-sanitizer dispenser—a perceptual cue that makes salient the threat posed by bacterial infections. Results revealed more conservative attitudes in the latter condition. This experiment did not include a control group of the sort necessary to determine whether the effect was specific to the threat of disease, or may reflect the perception of threats more generally. So although there is evidence linking activation of the behavioral immune system to political conservatism, it remains to be determined the extent to which these particular effects are psychologically distinct from effects that other self-protective motivational systems might also plausibly have on political conservatism.

5. Additional Consequences and Broader Conceptual Implications

In the preceding section, we summarized a rapidly growing body of evidence that documents many different ways in which activation of the behavioral immune system affects many different kinds of social psychological phenomena. In this section, we lift our gaze from these specific psychological outcomes and attend to some broader implications. We identify several ways in which some of the specific social psychological effects (reviewed above) can have further consequences that transcend the usual scope of social psychological inquiry—consequences for health outcomes, political decision-making, and the origins of culture. We also discuss how research on the behavioral immune system provides a useful means of conceptually integrating a wide range of superficially different social psychological phenomena, and how it connects to a broader conceptual perspective linking motivation to social cognition.

5.1. Human Health Outcomes

The behavioral immune system facilitates a wide range of affective, attitudinal and behavioral responses that are likely to have inhibited individuals' exposure to infectious diseases—and thus to have been associated with better health outcomes—under the ecological conditions within which ancestral populations evolved. Some of those same health benefits may still occur within modern human populations. The emotion most closely associated with the behavioral immune system—disgust—is associated with safe sex behaviors, hand hygiene behaviors, and other behaviors that inhibit the transmission of infectious diseases (Porzig-Drummond, Stevenson, Case, & Oaten, 2009; Scott, Curtis, Rabie, & Garbrah-Aidoo, 2007; Tybur et al., 2011). Reduced attitudinal inclinations toward sexual promiscuity and social gregariousness are also likely to be associated with reduced exposure to sexually- and socially-transmitted diseases (Burk, Ho, Beardsley, Lempa, Peters, & Bierman, 1996; Nettle, 2005). These beneficial effects may not only manifest in individuals' own individual health outcomes, but also—because of the epidemiological implications of individuals' actions—in the health outcomes of entire populations.

Less obviously, however, some of the social psychological phenomena associated with the behavioral immune system may also have *negative* health implications (Schaller, Murray, & Bangerter, 2015). Consider, for example, relations between disease threat, social gregariousness, and health. Because activation of the behavioral immune system is associated with reduced social gregariousness, people who feel chronically vulnerable to disease may have relatively small networks of friends and acquaintances. These people may consequently be at greater risk for loneliness and insufficient social support, both of which are associated with poorer long-term health outcomes (mostly through increased risk of *non*-infectious diseases such as cardiovascular disorders; Cacioppo, Hawkley, & Berntson, 2003; Cohen, 2004; Hawkley & Capitanio, 2015). The positive prophylactic consequences of reduced gregariousness may have outweighed these negative health outcomes under ecological conditions within which the behavioral immune system evolved, in which life spans were relatively short and the prevalence of infectious diseases was relatively high. But the negative health implications associated with reduced sociality may be more costly in modern societies in which life spans are long and the health risks posed by infectious diseases are more modest.

Similarly, conformity to local cultural norms and traditions may have been a beneficial means on inhibiting infection throughout much of human evolutionary history, but these benefits may be negligible within many contemporary societies in which the risks of infection, as well as the harmful consequences of infection, are mitigated by modern technological advances (e.g., vaccines, antibiotic medications). Indeed, in modern societies, conformist attitudes—which can promote superstitious adherence to traditional practices and reluctance to adopt novel technologies—may be quite costly. An illustrative example occurred during the AIDS epidemic in Africa: South African government officials persisted in promoting traditional dietary remedies (e.g., beetroot, garlic, beer) as a treatment for AIDS, while opposing more effective antiretroviral therapies (Kalichman, 2009).

Xenophobia too can have negative health implications in contemporary contexts, in part because it may lead people to be suspicious of aid from foreign peoples. For example, in 2003, distrust of Western governments apparently led government officials in several states in Nigeria to boycott a polio vaccination program sponsored by the World Health Organization (Jegede, 2007). As this example illustrates, the negative health consequences of xenophobia may manifest especially in developing nations that stand to benefit most from health-relevant assistance from foreign nations and transnational organizations. More recently, near the peak of the Ebola outbreak in West Africa in 2014, many towns and villages actively blocked outside healthcare workers from providing treatment, or sometimes from even entering regions entirely. Many locals cited both a distrust of foreign individuals and wariness of nontraditional medicine for refusal of treatment—indeed, many believed that these foreign entities were *causing*—rather than treating—the outbreak (Nossiter, 2014).

The broader implication is this: Because of their favorable effects on the risk of infection, the social psychological manifestations of the behavioral immune system may have some beneficial consequences for human health outcomes, and these benefits may be realized most readily under ecological circumstances that most closely mimic the ecologies within which anatomically-modern humans evolved. But, these social psychological phenomena may lead to additional outcomes too, some of which may have negative consequences for human health outcomes. These negative consequences are perhaps most likely to emerge under ecological conditions that differ from the ecologies in which humans evolved—in terms of lifespan, in terms of social structure, in terms of the prevalence of infectious diseases, and in terms of the methods available to mitigate the actual threat posed by those diseases.

5.2. Political Decision-Making and Public Policy

The behavioral immune system influences many of the everyday behavioral decisions that individuals make, and some of these decisions can have long-lasting consequences. Illustrative examples are provided by research linking the behavioral immune system to decision-making in the arena of politics and public policy.

Much research reveals that physical appearance matters in the context of political elections: Voters are more likely to vote for candidates who are more physically attractive (e.g., Berggren, Jordahl, & Poutwaara, 2010). Given the finding that people show stronger preferences for attractive faces under conditions in which the threat of disease is salient (Little et al., 2011; Young et al., 2011), it follows that the appearance-based voting bias is likely to also be exaggerated when the threat of disease is highly salient to voters. Recent research reveals this to be the case (White, Kenrick, & Neuberg, 2013). In one experiment, American participants first read one of three different stories—one that described no threat of any kind, another that made a predatory threat salient (and therefore elicited fear), and another that made the threat of infection salient (and elicited disgust). Shortly afterwards, participants were presented with photographs of British politicians who were either physically attractive or relatively unattractive, and were asked to indicate how likely they would be vote for each candidate in an election. Results revealed generally greater intentions to vote for physically attractive (compared to unattractive) candidates. More notably, this effect was especially large under conditions in which the threat of infectious disease was psychologically salient—even compared to the condition in which a different kind of threat was salient. These experimental results are conceptually complemented by results of actual election outcomes. White et al. (2013) conducted an analysis of U.S. congressional elections held in 2010, and found that physically attractive candidates were especially likely to win elections held in congressional districts characterized by relatively poor health outcomes.

In addition to its consequences for face preferences, activation of the behavioral immune also has consequences for the endorsement of conservative social and political attitudes (Terrizzi et al., 2013). It may therefore influence voting decisions based on candidates' political platform or party affiliation. Some support for this implication is offered by Brenner and Inbar (2015), who found that Dutch voters who were more prone to experience pathogen disgust were more inclined to vote for a socially conservative political party (*Partij Voor de Vrijheid*).

In addition to its potential influence on voter decision-making (and election outcomes), the threat of infection may also have implications for the decisions made by people who have already been elected. These decisions may manifest in the laws and public policies enacted by governments. Some relevant evidence has emerged from studies that treat geographical regions (rather than individuals) as units of analyses: In regions characterized by chronically greater prevalence of infectious diseases, governments tend to be more highly authoritarian. For example, across a culturally diverse range of small-scale societies—the kinds of populations traditionally studied by ethnographers—disease prevalence predicts authoritarian governance, and it does so uniquely, even controlling for other threats to human health and welfare (Murray, Schaller, & Suedfeld, 2013). An analysis of contemporary geopolitical units (nations) reveals the same pattern (Thornhill, Fincher, & Aran, 2009). Additional analyses reveal that this nation-level relation between disease prevalence and authoritarian governance is statistically mediated by nation-level mean scores on measures of individuals' authoritarian attitudes (Murray et al., 2013)—a pattern of results consistent with an interpretation that the prevalence of infectious diseases influences the attitudes held by individuals living within those ecologies, and these attitudes in turn have implications for the style of governance that emerges and persists within those societies.

5.3. Origins of Cultural Differences

The results linking disease prevalence to authoritarian governance do more than merely highlight implications that the behavioral immune system may have for political outcomes; these results also highlight implications that it may have for the origins of cultural differences more broadly.

The line of reasoning is as follows: Under conditions in which disease-causing pathogens are more highly prevalent, people are likely to be more chronically aware of, and to feel more chronically vulnerable to, the threat posed by infectious diseases. And so, compared to geographical regions characterized by a low prevalence of infectious diseases, in regions characterized by high prevalence of infectious diseases, the individual-level psychological outcomes associated with disease threat (e.g., higher levels of xenophobia, conformity, and preference for attractive faces; lower levels of extraversion; etc.) are more likely to be observed within these entire regional populations. Because variation in the prevalence of infectious diseases is influenced by meteorological and ecological conditions that are fairly enduring (Guernier, Hochberg, & Guégan, 2004), these population-level differences in psychological outcomes are likely to be fairly enduring as well, and thus manifest as cultural differences. The intriguing implication is that many worldwide cultural differences—in personality, values, and behavior—may be partially the product of psychological responses to the threat of infection.

Supporting this line of reasoning are the results of many studies that treat geographical regions as the unit of analysis and, collectively, reveal that many different aspects of cultural variation are correlated with ecological variation in disease prevalence. These correlations mimic the effects of disease threat on individual-level psychological outcomes. Just as the temporary salience of disease threat leads individuals to express more exaggerated xenophobic attitudes, the regional prevalence of infectious diseases correlates positively with population-level indicators of racial intolerance and ethnic violence (Letendre, Fincher, & Thornhill, 2010; Schaller & Murray, 2010). Just as the temporary salience of disease threat leads individuals to show preferences for attractive faces, the regional prevalence of infectious diseases correlates positively with population-level preferences for attractive faces (DeBruine, Jones, Crawford, Welling, & Little, 2010; Gangestad & Buss, 1993). Just as the temporary salience of disease threat leads women to express less promiscuous sexual attitudes, the regional prevalence of infectious diseases correlates negatively with the extent to which women within a population generally express promiscuous sexual attitudes (Schaller & Murray, 2008). Just as the temporary salience of disease threat leads individuals to report lower levels of extraversion, the regional prevalence of infectious diseases correlates negatively with mean levels of extraversion expressed within a population (Schaller & Murray, 2008). Just as the temporary salience of disease threat leads individuals to be more conformist in their own behavior and to be less tolerant of others' nonconformity, the regional prevalence of infectious diseases correlates positively with population-level measures of conformity and intolerance for non-conformity (Murray, Schaller, & Trudeau, 2011). And just as the temporary salience of disease threat influences moral judgments of others' transgressions, the regional prevalence of infectious diseases correlates positively with population-level measures of moral values (especially values pertaining to purity, group loyalty, and respect for authority; Van Leeuwen, Park, Koenig, & Graham, 2012).

Some of these specific cultural differences (including group loyalty and intolerance for nonconformity) are relevant to the broader, multifaceted concepts of individualism and collectivism. In fact, regional variation in disease prevalence is very strongly correlated with measures assessing cultural variation in individual and collectivism: In regions characterized by a higher prevalence of infectious diseases, cultures are more highly collectivistic (Fincher, Thornhill, Murray, & Schaller, 2008). The intriguing implication is that cultural differences in individualism and collectivism—differences that are fundamental to so much research in cultural psychology—may exist in part because of regional differences in the prevalence of disease-causing pathogens.

These studies of cross-national differences are necessarily correlational and so must be interpreted with inferential caution. Still, it is notable that the effects summarized above emerged even when controlling for economic and demographic variables that are commonly assumed to underlie cross-cultural differences in psychological outcomes. Furthermore, some of these studies—including studies assessing cultural differences in extraversion, conformity, and collectivism (e.g., Fincher et al., 2008; Murray et al., 2011; Schaller & Murray, 2008)—also employed methods to assess the prevalence of other threats to human welfare, and found that even when controlling for these other threats, the prevalence of infectious diseases was a unique predictor of cultural differences (for reviews, see Murray, 2014a, and Schaller & Murray, 2011).

If, as these results suggest, the behavioral immune system does have implications for cultural differences in attitudes and values, it may have further implications for societal outcomes—including economic outcomes—that follow from these cultural attitudes and values. For instance, based on results linking disease-threat to conformist attitudes, one might speculate that the threat of disease may inhibit discovery or adoption of technological innovations, some of which may be economically beneficial. Some evidence supports this hypothesis. Across a sample of 161 countries worldwide, ecological variation in the prevalence of infectious diseases negatively predicted four different nation-level indicators of scientific and technological innovation—and did so uniquely even when statistically controlling for other economic and demographic variables that influence innovation (Murray, 2014b).

5.4. Deeper Conceptual Insights into Social Psychological Phenomena

In our summary of empirical evidence, above, we drew attention to its implications for a wide range of social psychological phenomena. This body of research not only has *broad* implications, but also *deep* implications: It has led to deeper understandings of specific social psychological phenomena. Consider prejudice, for example. Prejudice has traditionally been conceptualized as a negative attitude toward social groups (and the members of those groups). That conceptualization has proven useful, but it is somewhat oversimplified. It ignores the fact that distinct forms of prejudice are associated with distinct motivational considerations. Compared to circumstances characterized by other forms of threat, when individuals perceive people who appear to pose an infection risk, they experience a unique form of prejudice—defined by the arousal of a particular emotional experience (disgust), and by the activation of specific kinds of cognitions into working memory (e.g., Park et al., 2007; Ryan et al., 2012). Furthermore, this functionally distinct form of prejudice is moderated by a functionally specific set of contextual variables—with novel implications for interventions that might effectively reduce prejudice (Huang et al., 2011). This body of evidence has been instrumental in the emergence of a more nuanced perspective that recasts the psychological study of prejudice as the psychological study of prejudice*s* (Schaller & Neuberg, 2012).

A similar story emerges from research linking the behavioral immune system to the subjective appeal of attractive faces. Faces are more attractive when they are more psychophysically prototypical; and people find prototypical stimuli to be more appealing, in part, because they are easy to perceptually process (Winkielman, Halberstadt, Fazendeiro, & Catty, 2006). But although perceptual fluency may contribute to the appeal of attractive faces, it is not the only contributing factor. The motivational psychology of disease avoidance also plays a role. Activation of the behavioral immune system leads to an exaggerated preference for attractive faces—an effect that is specific to faces (Young et al., 2011)—and this effect is especially pronounced in contexts that have especially pronounced fitness implications (Little et al., 2011; White et al., 2013). Thus, just as there are multiple psychological mechanisms that contribute to prejudice, there are also multiple mechanisms that contribute to the subjective attractiveness of attractive faces. Analogously, just as there are demonstrably different kinds of negative responses that can be described as prejudice, there may also be subtly different kinds of positive responses that constitute facial attraction.

Prejudice and attraction are often treated as distinct categories of social psychological phenomena. They are typically studied by different groups of scholars, are covered in different chapters of textbooks, and are subject to different explanatory models and theories. But at a deeper level there are many similarities and conceptual connections between the psychological bases of prejudice and the psychological bases of attraction. Research on the behavioral immune system helps highlight some of those similarities and therefore provides a useful conceptual bridge between these (and other) superficially distinct kinds of social psychological phenomena.

Research on the behavioral immune system also offers a conceptually integrative perspective on a variety of phenomena pertaining to cultural norms—including behavioral conformity to perceived norms, conservative political attitudes regarding the perpetuation of norms, and moral judgments about individuals who violate norms. Each of these phenomena is influenced by a variety of conceptually different psychological processes, including motivational processes that are independent of disease avoidance—such as the need for belongingness (which influences conformity; Williams, Cheung, & Choi, 2000) and the desire for cognitive closure (which influences conservatism; Jost et al., 2003)—as well as other psychological processes (e.g., causal reasoning processes that influence moral judgments; Cushman, Young, & Hauser, 2006). For this reason, perhaps, these topics are rarely integrated into a common conceptual framework. Recently, however, research on disgust has been instrumental in illuminating conceptual connections between moral judgments and political attitudes (Haidt & Graham, 2007; Helzer & Pizarro, 2011). At a deeper level of analysis, it appears that conformity, conservatism, and moral judgment are conceptually connected because of the disease-buffering benefits of social norms (Fabrega, 1997)—with the consequence that conformity, conservatism, and moral judgments are all motivated, in part, by the psychology of disease avoidance.

5.5. The "Old Look" at Human Motivation and Social Cognition

For decades, social psychological research has produced prototypical examples of motivated perception and motivated cognition—the kinds of phenomena that, at the outset of the cognitive revolution, characterized the so-called "New Look" approach to perception (Bruner, 1957, 1992). But it is only very recently that social psychologists have begun to attend to the motivational psychology of disease avoidance and its unique implications for social cognition. Why did it take so long? One reason, perhaps, is that the scholarly attention of social psychologists tends to be captured by topics that are of obvious importance in the here and now. For most social psychologists, the "here and now" is characterized by modern *technological* solutions to the ancient problem of parasite infection, and this makes it is easy to overlook the likelihood that *behavioral* solutions were of profound importance to survival and fitness throughout most of human history.

Because of this natural—and potentially limiting—tendency to focus on the problems faced by modern peoples living in technologically sophisticated societies, useful scholarly benefits can accrue from the application of evolutionary principles to human motivation and cognition. A rigorous evolutionary approach logically compels one to lift one's gaze from the here and now, to identify fitness problems that characterized the ecologies within which the human nervous system actually evolved, and to further identify psychological mechanisms that might plausibly have evolved as solutions to those prehistoric problems. The logical principles of this evolutionary approach (e.g., the cost/benefit analyses that underlie the smoke detector principle and the functional flexibility principle) have been instrumental in guiding research on the behavioral immune system. This research exemplifies a broader thematic body of research that links the psychological principles of motivated cognition with a logical analysis of evolution within ancient ecologies—a version of the "New Look" that has been nicknamed, cheekily, the "Old Look" (Kenrick, 2012).

Unlike much other work on motivated cognition, the "Old Look" is characterized not merely by the identification of transient goal states that influence perception and cognition, but by a conceptual linkage between goal states and underlying motivational systems that evolved as means of solving specific problems—perils to be avoided or prospects to be attained—that had implications for reproductive fitness in ancestral ecologies. It is characterized also by the specification of behavioral responses that would have had functionally beneficial implications for the solution of those problems, and by the further specification of cognitive responses—including perceptual biases and specific kinds of stimulus-response associations—that might plausibly have evolved as a means of facilitating those adaptive behavioral responses. The "Old Look" has proven to be a highly generative approach to psychological science. One way that it has been generative is by yielding novel empirical discoveries linking specific goal states to cognitive outcomes, some of which are counterintuitive and perhaps even inexplicable in the absence of an evolutionary perspective on motivation. (An illustrative example is provided by research on the arousal of self-protective goals and its implications for enhanced recognition memory for outgroup faces; Ackerman et al., 2006; Becker et al., 2010). Another way that it has been generative is by drawing attention to—and facilitating research on—motivational systems that have social psychological implications, but which have mostly been ignored within the social psychology literature. (Recent research on the parental care motivational system, for example, reveals that this system has implications for many different kinds of social psychological outcomes, including moral judgments, mate preferences, and biased impression formation, even among non-parents; Buckels, Beall, Hofer, Lin, Zhou, & Schaller, 2015.) Research on the behavioral immune system attests to the generative utility of the conceptual principles that define the "Old Look."

6. Unanswered Questions and Directions for Future Research

Compared to other behavioral scientists—such as behavioral ecologists who have spent decades studying the behavioral avoidance of infection risk in non-human species—psychological scientists were late to appreciate the profound impact that disease-causing parasites, and the need to avoid them, can have on social behavior. Despite this late start (or perhaps because of it), the last dozen years has been characterized by rapid progress in our understanding of the behavioral immune system and its many social psychological implications. Still, there is a lot that we do not know. In the last section of this article, we draw attention to a set of unanswered questions that may guide future research on the behavioral immune system.

6.1. Appraisal Processes

Psychological research on the behavioral immune system has mostly focused on psychological *responses* to disease-connoting stimuli. This focus on stimulus-response phenomena largely ignores processes through which stimuli are *appraised* as connoting some sort of threat in the first place. This is an important conceptual distinction. Much of the evidence that we have reviewed shows that there are unique psychological consequences that follow from the appraisal of some sort of disease threat; but this does not imply that there must also be a unique set of psychological mechanisms dedicated specifically to the detection and appraisal of things that might pose a disease threat. Indeed, as others have suggested, initial appraisal of disease threat may often be accomplished through a more broadly-applicable set of sensory and inferential mechanisms that are able to detect, and appraise, threats of many different kinds (Boyer & Lienard, 2006; Woody & Szechtman, 2011).

However, even if a common set of general-purpose mechanisms are often employed in the service of appraising different kinds of threat, there may also be additional, functionally-specific adaptations that facilitate the detection of specific threats—such as the threat of infectious disease. Any such disease-specific appraisal mechanisms may operate within the context of specific sensory modalities. For instance, many mammals employ olfactory cues to identify potentially-infectious conspecifics; and specific genes—which code for specific neurochemical mechanisms—facilitate the detection of those olfactory cues (Kavaliers, Choleris, & Pfaff, 2005). Analogous adaptations may exist in humans (Olsson et al., 2014). It remains for future research to more fully explore whether the unique motivational psychology of disease avoidance might also be associated with domain-specific appraisal mechanisms.

6.2. The Role of Disgust

The emotional experience of disgust is the affective signature of the behavioral immune system. Disgust is aroused by many stimuli that are appraised as connoting an immediate infection risk, and the subjective experience of disgust is associated with many of the actions and attitudes (e.g., behavioral avoidance, moral condemnation, xenophobia) that are influenced by the behavioral immune system. Given this tight connection, it has been argued that the behavioral immune system is isomorphic with disgust (e.g., Lieberman & Patrick, 2014)

This argument is predicated upon a computational conceptualization of emotions that treats conventional distinctions between affect and cognition as unnecessary historical anomalies (Lieberman & Patrick, 2014). Within such a framework, "disgust" represents far more than a transient subjective emotional experience, encompassing the full set of evolved mental mechanisms that allow that transient state to be experienced in response to infection risks, and that facilitate adaptive psychological responses. In terms of analytic rigor, this kind of conceptualization has a lot to recommend it. And if one adopts this computational conceptualization of disgust, then "disgust" is indeed conceptually inseparable from the "behavioral immune system."

Most people—including most psychological scientists—do not conceptualize disgust in that way, and instead employ the word to refer to a specific kind of transient emotional state. This is the way in which we have used the word here. And it is with this more typical meaning in mind that it is worthwhile to ask this question: To what extent does the subjective experience of disgust play an actual causal role in producing the various social psychological phenomena reviewed above?

In addressing this question, it may be useful to recognize that the behavioral immune system produces responses that vary in terms of the extent to which they are *reactive* versus *proactive* (Schaller, 2014). Reactive responses are characterized by aversive responses to stimuli that, on the basis of perceptual cues, connote an immediate risk of infection. In contrast, proactive responses may occur even in the absence of any perceptual evidence of an immediate infection risk, and are characterized by attitudes and behaviors that help to manage a latent disease threat, thereby reducing the likelihood that the latent threat actually manifests in a way that might require reactive avoidance. Some of the phenomena facilitated by the behavioral immune system are highly reactive, such as when the sight of a disfigured face elicits avoidant behavior (Ryan et al., 2012). Other phenomena are more proactive, such as the tendency to conform to majority opinion (Murray & Schaller, 2012). Other phenomena—such as xenophobic attitudes elicited by the perception of subjectively foreign peoples (Faulkner et al., 2004)—might be considered to lie somewhere on a continuum in between.

It seems clear that the arousal of disgust is especially likely to occur in conjunction with the most clearly reactive responses. Indeed, Ryan et al. (2012) found that individuals' unwillingness to touch objects (including disfigured bodies) was very highly correlated with the intensity of the disgust response to those objects. In contrast, conformist responses to majority opinion are not typically accompanied by the subjective experience of disgust.

But even though the disgust may be acutely aroused in the context of highly reactive response, it may *not* be a necessary causal antecedent of those reactive responses. And even though disgust may not be aroused in the context of many proactive responses, it may nonetheless play a crucial causal role in producing those proactive responses. Both of these speculative observations may seem a bit counterintuitive, and so they merit some explanation.

The first piece of speculation is simply a straightforward implication of the broader observation—which dates back at least to William James (1890)—that many emotional responses are coincident with, rather than causally antecedent to, motor responses. Some empirical evidence also suggests that disgust may simply be concurrent with, rather than causally antecedent to, reactive avoidance. Ryan et al. (2012) varied the extent to which stimuli connoted an infection risk, and found that this manipulation influenced both subjective reports of disgust and also behavioral avoidance of contact; but the latter effect was stronger than the former effect—a difference in relative effect sizes that is exactly the opposite of what one would expect if disgust was a causal antecedent of avoidant responses.

The second piece of speculation requires a bit more unpacking. How is it that the disgust may play an important causal role in producing proactive responses that, when they occur, are unaccompanied by disgust? The argument is predicated upon the premise that—because of its effects on learning and memory (e.g., Chapman et al., 2013; Stevenson, Oaten, Case, Repacholi, & Wagland, 2010)—the temporary arousal of disgust at any one moment in time may have causal implications for formation of attitudes and other knowledge structures that endure long into the future. For example, disgust may be temporarily aroused by the observation of a behavior that violates local cultural norms (e.g., someone defecates in a place that they shouldn't), and this immediate affective response may facilitate the acquisition of attitudinal antipathy toward nonconformity as well as a positive attitude toward conformity. This positive attitude toward conformity is likely to facilitate one's own actual conformity behavior in the future. This conformity behavior may be unaccompanied by any concurrent experience of disgust, but disgust nonetheless may have played an important causal role in the long-term causal sequence of events that produced that behavior.

It may be fruitful to develop lines of research that more fully examine the effects of disgust on attitude formation, and also examine further consequences for conformity and other proactive manifestations of the behavioral immune system. More generally, it will be useful to do research that more rigorously examines exactly when and how disgust is (and is not) causally implicated in the social psychological phenomena produced by the system (Schaller, 2014). Doing so will contribute to the psychological literature linking disgust to contemporary human behavior, and may also contribute to a broader, multi-disciplinary conversation regarding the evolutionary history of disgust and the role played by infectious diseases in that evolutionary history (Clark & Fessler, 2014a; Rozin et al., 2009; Tybur et al., 2013).

6.3. Connections to Other Forms of Anti-Parasite Behavioral Defense

We have used the term “behavioral immune system” to refer to a specific kind of motivational system—a set of psychological mechanisms that, when activated, facilitate behavioral responses that, throughout much of human history, are likely to have reduced individuals’ contact with disease-causing parasites. The responses motivated by this psychological system are not the only behavioral means by which humans and other animals defend against the threat posed by infectious diseases. For example, there is also a large literature on “sickness behavior,” which documents specific ways in which the behavioral tendencies of people (and other animals) change following infection, as a means of facilitating recovery from that infection (e.g., Dantzer & Kelley, 2007; Eisenberger, Inagaki, Mashal, & Irvin, 2010; Inagaki, Muscatell, Irwin, Moieni, Dutcher, Jevtic, Breen, & Eisenberger, 2015). There is a separate literature—based substantially upon observations of non-human primates—that documents the ingestion of medicinal plants as a means of facilitating recovery from parasitic infections and, sometimes, inhibiting incidence of new infections (Huffman, 1997, 2001).

Although sickness behavior and medicinal plant ingestion do appear to be evolved behavioral strategies that complement—and compensate for the limitations of—immunological defenses, these behavioral outcomes do not appear to be products of the same psychological system that we have focused on here. The behavioral tendencies associated with sickness behavior are not prophylactic responses precipitated by the perceived risk of future infection; rather, they are reactions to infections that have already occurred. And the underlying neurophysiological mechanisms—which involve the immune system's production of pro-inflammatory cytokines (Dantzer & Kelley, 2007)—are almost certainly distinct from those underlying the social psychological phenomena that we have reviewed above. Similarly, although the ingestion of some medicinal plants may proactively inhibit parasitic infections, this prophylaxis seems likely to be the product of a conceptually distinct set of adaptations that are specific to a different motivational system—the appetitive system—that governs the kinds of foods that organisms find palatable.

Of course, these apparent differences may be misleading. There are also many apparent differences between prejudice, sexual attitudes, and conformity to social norms; and, yet, as we have discussed above, these superficially different social psychological phenomena are all influenced by a common motivational system—the behavioral immune system—that serves the function of anti-parasite defense. Perhaps there are deeper commonalities linking this motivational system to sickness behavior, self-medication, and other forms of anti-parasite behavioral defense as well. An important agenda for future research is to more rigorously identify the extent to which various behavioral defenses against infectious diseases are, and are not, governed by the same set of underlying mechanisms.

6.4. Connections to the "Real" Immune System

Immunological defenses and behavioral defenses can sensibly be perceived as complementary sets of adaptations to the fitness problem posed by parasites. But, as illustrated by research on cytokine-mediated sickness behavior (Dantzer & Kelley, 2007), there are important causal linkages between immunological responses and behavior. Analogously, several lines of evidence suggest that the psychological mechanisms underlying the behavioral immune system may have implications for the "real" immune system, and vice versa.

One line of research draws upon the principle of functional flexibility and examines specific ways in which psychological phenomena associated with the behavioral immune system are exaggerated under conditions in which individuals' immunological defenses are temporarily compromised. Some research indicates that avoidant responses to disfigured people are exaggerated among individuals who are recovering from recent acute infections (Miller & Maner, 2011). Other studies show that during the first trimester of pregnancy—when immunological responses to infection are suppressed—women exhibit elevated sensitivity to disgust and more exaggerated ethnocentric attitudes (Fessler, 2002; Fessler et al., 2005; Navarette et al., 2007). More generally, anytime levels of the hormone progesterone are elevated—as occurs during certain phases of the menstrual cycle—immune function tends to be suppressed, and this may have consequences for a wide range of phenomena associated with the behavioral immune system. One set of studies found that women expressed more exaggerated preferences for healthy faces (compared to unhealthy faces) when progesterone levels were elevated (Jones, Perrett, Little, Boothroyd, Cornwell, Feinberg, Tiddeman, et al., 2005). Similarly, Fleischman and Fessler (2011) found that women's salivary progesterone levels predicted disgust responses to disease-relevant images as well as several cognitions and behaviors that may serve a disease-avoidant function.

A second line of research examines individual differences in the genetic bases of immunocompetence and their relation to individual differences in behavioral tendencies associated with the behavioral immune system. One recent study focused on the *IFNG* +874 gene, one allele of which is associated with greater susceptibility to infectious diseases such as malaria, tuberculosis, and leprosy. Results revealed that, compared to individuals who possessed a different allele, individuals who possessed the disease-risk allele showed generally lower levels of extraversion (MacMurray, Comings, & Napolioni, 2014). Another study focused on a different genetic polymorphism—the *ACP1* gene—that also has a specific allele associated with poorer immunological function. Individuals who possessed this particular allele tended to show lower levels of both extraversion and openness to experience (Napolioni, Murray, Comings, Peters, Gade-Andavolu, & MacMurray, 2014). Taken together, these studies suggest that genetic variants linked to chronically increased immunological vulnerabilities may also be associated with behavioral dispositions that help to mitigate those vulnerabilities.

A third line of research reveals that perceptual cues connoting increased risk of infection—the kinds of cues that stimulate a disgust response—also exert a causal influence on activation of the "real" immune system (Schaller, Miller, Gervais, Yager, & Chen, 2010; Stevenson, Hodgson, Oaten, Barouei, & Case, 2011; Stevenson, Hodgson, Oaten, Moussavi, Langberg, Case, & Barouei, 2012). For example, Schaller et al. (2010) examined immunological responses to infection (white blood cells' production of the proinflammatory cytokine interleukin-6) immediately following individuals' perceptual exposure to specific kinds of visual cues. In one condition, those visual cues connoted the imminent threat of infection (photographs of people showing evident signs of sickness); in a control condition, those visual cues connoted the imminent threat of violent attack (photographs of aggressive-looking men with guns). Results revealed that when perceptual cues connoted an especially high risk of imminent infection, individuals' white blood cells produced an especially potent inflammatory response to infection. Thus, it appears that psychological mechanisms regulating the magnitude of responses associated with the behavioral immune system also regulate the magnitude of immunological responses too.

Given these intriguing linkages, Clark and Fessler (2014b) suggested that work on the behavioral immune system could be considered a part of the broader discipline of psychoneuroimmunology. Gangestad and Grebe (2014) make an even stronger claim. They argue that from a rigorous evolutionary perspective—in which the capabilities and characteristics of organisms must be considered from the point of view of the genes that build those organisms as a means of reproducing themselves—the distinction between immunological and behavioral defenses is somewhat arbitrary and perhaps unnecessary. If so, then at some point in the future—after research on the behavioral immune system has more fully illuminated its many social psychological implications as well as its linkages with other forms of defense against infectious diseases—the apparent distinction between the behavioral immune system and the "real" immune system may have disappeared altogether, and will have been superseded by a more comprehensive and deeply-integrated understanding of the many ways in which the selection pressures posed by infectious diseases have shaped our human nature.

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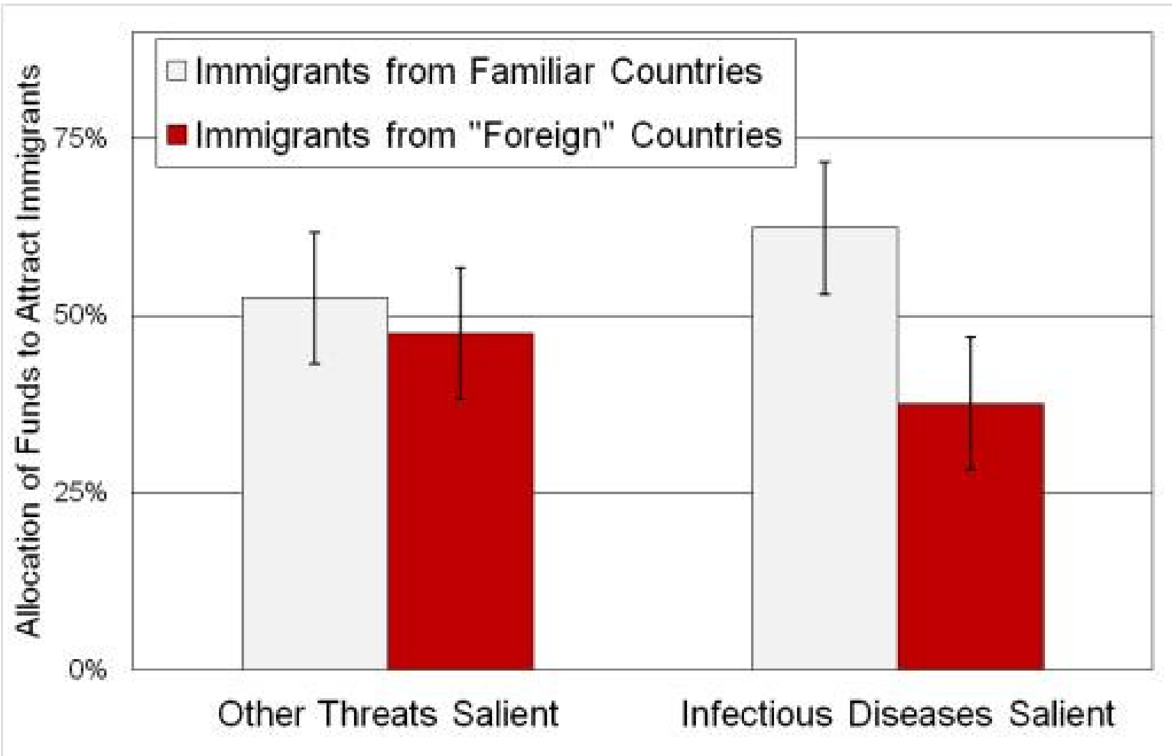
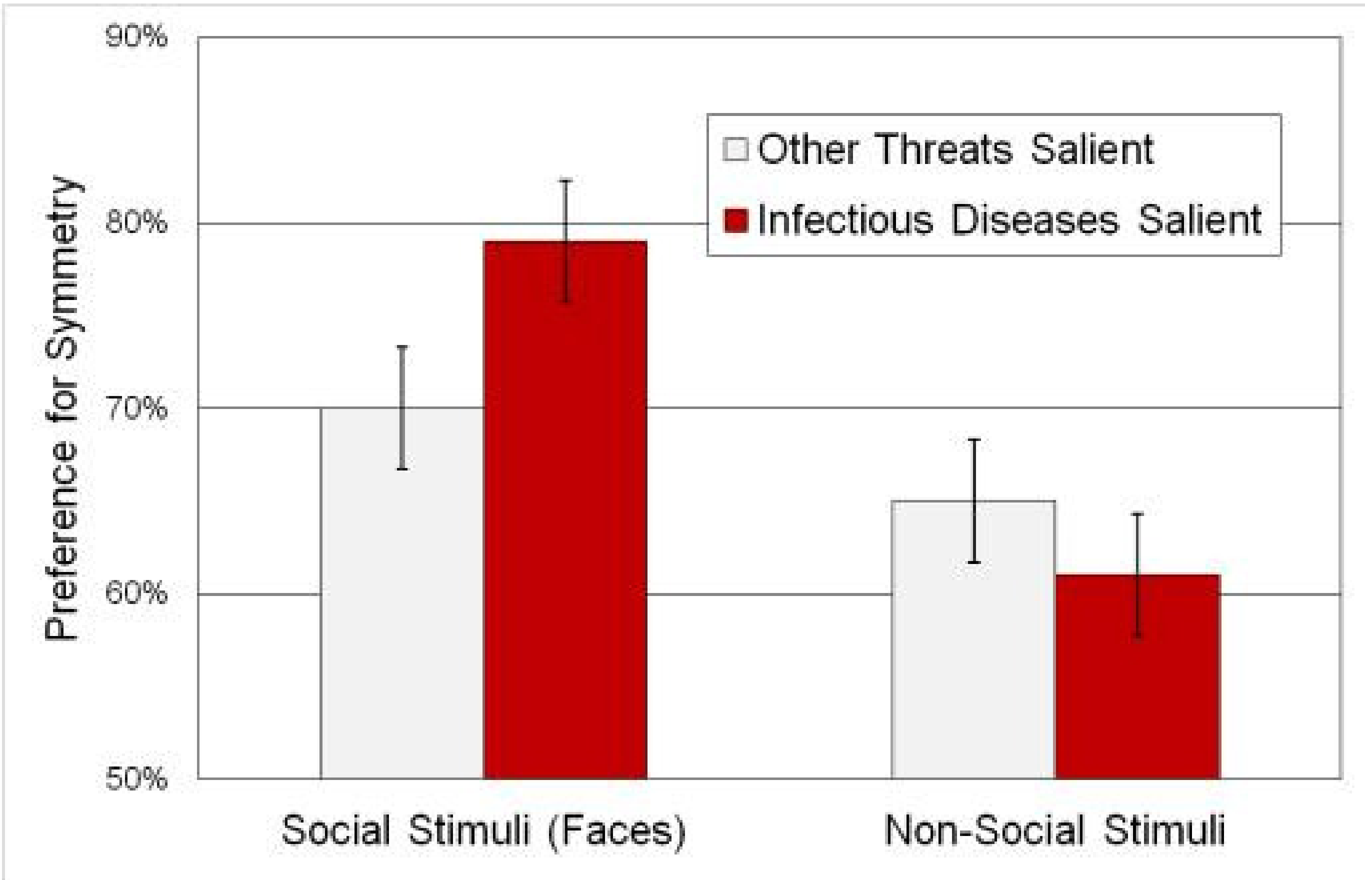
Figure Captions

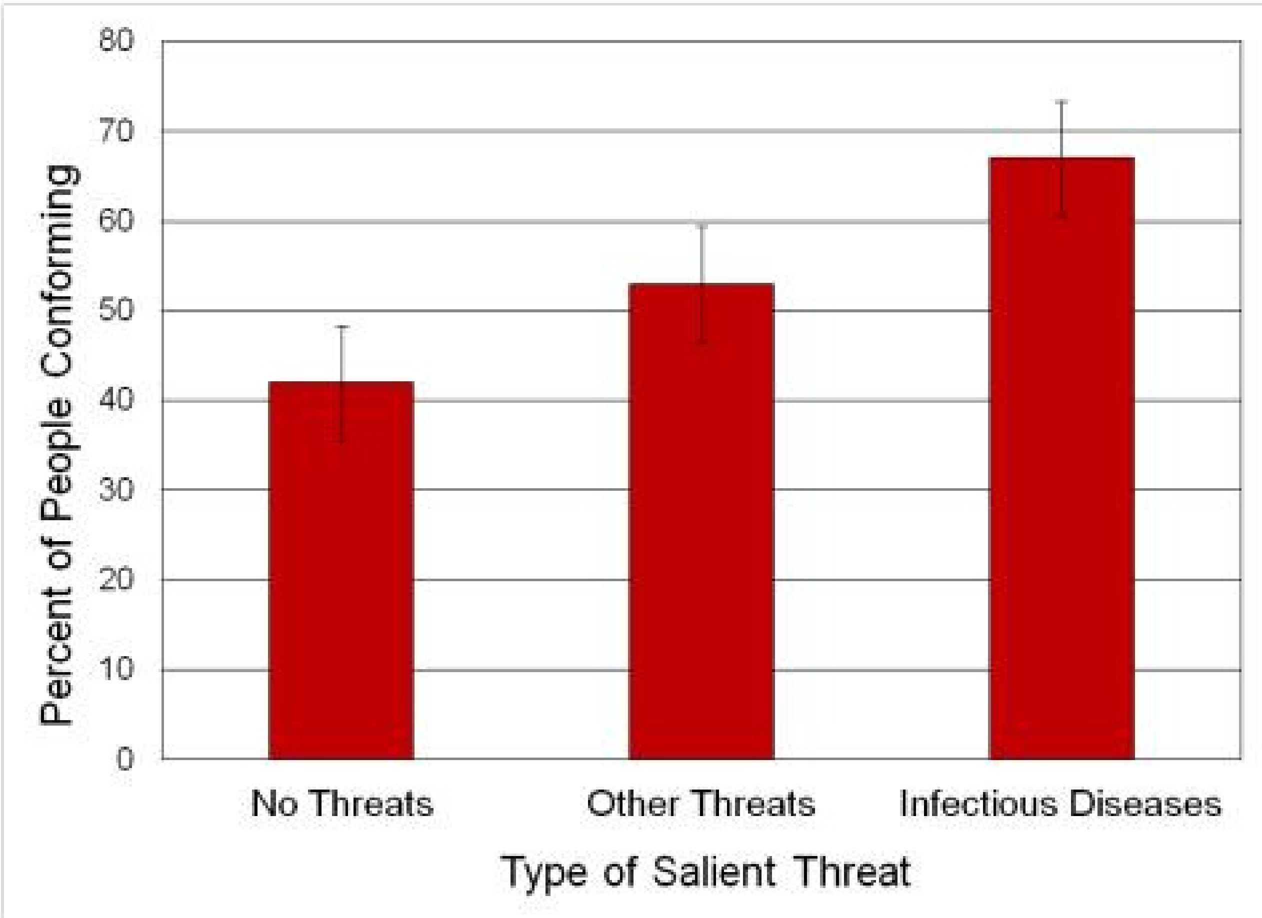
Figure 1. Results from an experiment testing the effect that the psychological salience of infectious diseases has on xenophobia (Faulkner et al., 2004). Canadian participants first watched a brief slide show in which either potentially fatal accidents or infectious diseases were made psychologically salient. Shortly afterwards, participants indicated the percent of government funds that they preferred to see allocated to recruit immigrants from countries that were either subjectively familiar (e.g., Taiwan) or subjectively foreign (e.g., Mongolia). Xenophobia is indicated by a greater allocation of funds to recruit familiar immigrants rather than foreign immigrants. Results show that—compared to the experimental condition in which other threats were salient—when the threat of infectious disease was temporarily salient, people exhibited more strongly xenophobic attitudes.

Figure 2. Results from an experiment testing the effect that the psychological salience of infectious diseases has on the perceived attractiveness of symmetrical faces (Young et al., 2011). Participants first watched a brief slide show in which either potentially fatal accidents or infectious diseases were made psychologically salient. Shortly afterwards, participants were presented with a series of trials on which they indicated which of two stimuli was more pleasing to look at. On some trials these stimuli were faces, one of which was symmetrical and one of which was asymmetrical. On other trials these stimuli were non-social stimuli, one of which was symmetrical and one of which was asymmetrical. A greater preference for symmetry is indicated by a higher percent of trials on which the symmetrical option was chosen. Results show that—compared to the experimental condition in which other threats were salient—when the threat of infectious disease was temporarily salient, people exhibited an exaggerated preference for symmetrical faces. No such effect emerged on preferences for non-social stimuli.

Figure 3. Results from an experiment testing the effect that the psychological salience of infectious diseases has on conformity to majority opinion (Murray & Schaller, 2012). Participants first engaged in a guided recall task in which they reflected upon either (a) a non-threatening event, (b) an event that made them feel vulnerable to non-disease-related threats, or (c) an event that made them feel vulnerable to infectious disease. Shortly afterwards, they were presented with a task on which they had the opportunity to express an opinion that either conformed to the apparent majority opinion, or deviated from it. Results show that—compared to other experimental conditions (including the condition in which other threats were salient)—when the threat of infectious disease was temporarily salient, a higher percentage of people conformed to the majority opinion.


Immigrants from Familiar Countries
Immigrants from "Foreign" Countries
Allocation of Funds to Attract Immigrants
75%
50%
25%
0%
Other Threats Salient
Infectious Diseases Salient


90%
80%
70%
60%
50%
Preference for Symmetry
Other Threats Salient
Infectious Diseases Salient
Social Stimuli (Faces)
Non-Social Stimuli


80
70
60
50
40
30
20
10
0
Percent of People Conforming
No Threats
Other Threats
Infectious Diseases
Type of Salient Threat